

OBSERVATIONS ON THE SO-CALLED TRUMPETER IN
BUMBLEBEE COLONIES.¹

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About 250 years ago, the Dutch painter Goedart (1685) published a comprehensive treatise² on insects, volume 2 of which contains a unique and probably the oldest account of the life-history and habits of bumblebees. The account seems to be based almost entirely on the author's own observations, and is of interest chiefly because of its many naive anthropomorphisms. Thus, for example, Goedart (pp. 242-245) states that the members of a bumblebee colony, besides keeping a "king" like the honeybees, also have another individual among them which mounts to the top of the nest each morning about 7 A. M., and, like the bugler in the army, calls his companions to work by rapidly vibrating his wings, thereby producing a noise not unlike that of a drum. This performance, according to Goedart (p. 245), lasted for about a quarter of an hour each morning, and was observed repeatedly, not only by him, but also by others. About seventy-five years later, Goedart's (1685) observation was confirmed by the French Abbé Noël de Pluche (1764)³, but de Pluche (p. 185) found that the "drummer", or "trumpeter", which he had under observation, called his companions to work at 7.30 A. M., instead of 7.

No one seems to have questioned this fantastic story until 1742 (about 75 years after the story originated), when the great French engineer and entomologist, Réaumur (pp. 1-30), published his observations on bumblebees. Although this famous scientist had a large number of bumblebee colonies under observation, he was unable to discover any such behavior as that described

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²The first edition of this work appeared from 1662-1669, both in Dutch and in Latin. It was later also translated into English (1682) and French (1700).

³According to Sladen (1912, p. 48), other editions of this work appeared as early as 1732. Translations into English (by Samuel Humphreys (1740), German (1746), and Spanish (1754), made this comprehensive work accessible to a large number of readers outside of France.

by the earlier observers, and therefore came to the conclusion that Goedart's (1685) "trumpeter" story was a fable. Réaumur's (p. 30) opinion in this matter naturally carried much weight, being accepted by such eminent entomologists as Kirby and Spence (1818, p. 384), and dealt the bumblebee "trumpeter" a blow which was effective for almost 150 years, when Goedart's (1685) story was again revived by the well-known Austrian bumblebee student Hoffer (1881, 1882-83).

Being acquainted with the contradictory claims of Goedart (1685) and Réaumur (1742), Hoffer (1882-83, p. 23) tried for a number of years to find a "trumpeter" among the numerous bumblebee colonies which he had under observation, but his efforts were unsuccessful until the summer of 1881. On July 7 of that year, Hoffer (p. 23) obtained a strong colony of *Bremus (Bombus) ruderatus* which he placed in a window facing southeast. Early the following morning, Hoffer's (p. 24) attention was suddenly attracted by a peculiar humming in the new colony, and, upon investigating, he found that the sound was produced by one of the larger bees which was perched on the waxen envelope of the nest and was vigorously, but uniformly vibrating her wings. Overjoyed at having rediscovered the long-sought "trumpeter," Hoffer (p. 25) roused his wife and children, and later also called in the neighbors, to witness the interesting performance. However, Hoffer's (1882-83) "trumpeter," or "trumpeterette" as she ought to be called, evidently was somewhat of a slave-driver, and rather persistent, as compared with those of Goedart (1685) and de Pluche (1764), for "with painful regularity" she called her companions to work every morning shortly after three o'clock, and continued her "trumpeting" for about an hour. Hoffer (p. 25) now became interested to know what would happen if he removed the "trumpeter" from the colony, and, on doing so, found that thereafter the "trumpeting" was performed by another member of the colony, although about an hour later than before. As the colony grew smaller toward the end of the summer, the activities of the "trumpeter" became more and more irregular. This, and the fact that one of his former students claimed to have heard a "trumpeter" in a colony of *Bremus lapidarius*, led Hoffer (1882-83, pp. 25, 26) to the

conclusion that only *Bremus ruderatus*, and perhaps some other "hypogeic" species, have "trumpeters," but only while the colonies are strong.

Hoffer's (1882-83) confirmation again brought Goedart's (1685) "trumpeter" story into good repute among biologists for a period of more than twenty years. With apparently the single exception of Pérez (1889), it was accepted—in most cases after personal verification—by Firtsch (cf. Hoffer, 1882-83, p. 25), Kristof (1883), Härter (1890), Sharp (1899), Marshall (1902), and Bengtsson (1903). Pérez (p. 117), while not in the least doubting the general correctness of Hoffer's (1882-83) observations, rejected the latter's interpretation by pointing out (1) that there is little sense in having a "trumpeter" unless he be the first one to rise, and (2) that the sound produced by the "trumpeter" is of no use whatever, as far as rousing the colony is concerned, since (according to Pérez) bumblebees, like honeybees and ants, are completely deaf. Pérez (1889) then offers his own explanation. After expressing the opinion that the bumblebee "trumpeter" fulfills no social function, and that the "trumpeting" is probably done for his own benefit, Pérez (p. 117) suggests that the "trumpeters" in bumblebee colonies, like the so-called ventilators among honeybees, are newly-hatched individuals which are training their wing muscles for the long flights which they will soon make. However, as we have already seen, Pérez' (1889) theory, although more plausible than that of Goedart (1685), seems to have made little or no impression upon contemporary biologists.

Fourteen years after the publication of this theory, a third interpretation was offered by the well-known German bee student von Buttel-Reepen (1903, 1907). Unlike Pérez (1889), this author suggested that the bumblebee "trumpeter" has the same social function as the ventilators in the honeybee colony,⁴

⁴Since writing the above, I have discovered that a similar explanation was offered by Mr. J. Angus in a letter to Messrs. A. S. Packard and F. W. Putnam (cf. Packard (1868), 35 years before von Buttel-Reepen published his interpretation. Mr. Angus' letter partly reads as follows: "I have found the males [of *Bremus (Bombus) vagans*] plentiful near our garden fence, with a hole such as would be made by a mouse. They seem to be quite numerous. I was attracted to it by the noise they were making in fanning at the opening. I counted at one time as many as seven thus employed, and the sound could be heard several yards off. Several males were at rest, but mostly on the wing, when they would make a dash among the fanners, and all would scatter and sport around. The workers seem to be of a uniform size, and fully as large as the males. I think the object of the fanning was to introduce air into the nest, as is done by the Honey-bees."

namely, to reduce the temperature, or to expel moisture or bad odors from the nest. Similar conclusions were reached by the Norwegian biologist Lie-Pettersen (1906). This new interpretation was accepted—in some cases after extensive experimentation—by Stierlin (1906), Wagner (1907), Gundermann (1908), Lindhard (1912), and Sladen (1912).

However, within the last decade, Goedart's (1685) "trumpeter" story has found another adherent in Bachmann (1915, 1916). What is more, Bachman (1915) has discovered that the bumblebee "trumpeter", in addition to rousing the members of the colony in the morning, also attends to the "curfew" in the evening. This latter performance, Bachmann (1915, p. 87) describes as follows: "Um $\frac{1}{2}$ 9 Uhr begann der Hummeltrompeter sein Abendlied. Es war ein längerer Ton, unterbrochen von einem Triller ähnlich wie wenn ein Tier im Kästchen fliegen würde. Der Trompeter schlug aber nur, auf der Wabe stehend, die Flügel."

The activity of the bumblebee "trumpeter" in the morning is described very vividly by Bachmann (1916, p. 103) in the following words: "Genau um 6 Uhr erhebt sich ein Summen im Nest, das ununterbrochen 2 Minuten dauert. Ich musste gleich an den Hummeltrompeter denken, den Hoffer in einem Nest von *Bombus ruderatus* entdeckt hat. Dreimal setzt mein Musikant an, bis es lebendig wird und ein Tierchen zum Abflug erscheint. Um 6.26 bringt ein geschäftiges Weibchen eine grosse Larve geschleppt und der Trompeter übt unentwegt seine Kunst. Zuerst in gleicher Tonlage summend, werden, wenn es länger dauert, die Schwebungen höher und tiefer, vibrierend, dann stossweise wie das Geräusch des Wagnerschen Hammers oder bei der Entladung elektrischer Funken, endlich wie ein langsamer Trommelwirbel, bis der Ton etwas höher wird und dann langsam er stirbt.

"Mitunter höre ich deutlich die Flügel schlagen und meine dabei, es fliege eine Hummel nahe am Kopf vorüber. Dieses Wecken dauert von 6.44 bis 7.06, also 22 Minuten ohne Unterbrechung and ohne die geringste Störung meinerseits. Bis $\frac{1}{2}$ 8 Uhr höre ich noch dreimal einen kürzeren Ruf. Dann kriechen

gleich 3 Hummeln auf einmal aus dem Nestloch, nachdem mit Körbchen beladene im Tor vorher einpassiert waren und der Betrieb in der Hummelburg kommt in regen Gang."

These two passages would not have been written, had Bachmann (1915, 1916) paid more attention to the literature of the preceding decade. As we have already seen, Bachmann's (1915, 1916) assertions were contradicted years before, by statements published by several authors, notably von Buttel-Reepen (1903), Lie-Pettersen (1906), Wagner (1907), Lindhard (1912), and Sladen (1912). To these may be added certain observations and experiments of my own.

During the summers of 1921 and 1922, I had under observation about sixty *Bremus* (*Bombus*) colonies belonging to ten⁵ of our thirteen New England species, and have frequently had occasion to observe the behavior which gave rise to the "trumpeter" story. That the fanning of these so-called trumpeters has to do with ventilation of the nest, and not with rousing the colony, or the exercising of wing muscles, may be demonstrated very easily by exposing a bumblebee colony to the rays of the sun, a fact which was first pointed out by Lie-Pettersen (1906) and Wagner (1907). The conclusions which these two authors reached are corroborated by the following observations which were made during the summer of 1921.

Of the thirteen colonies which I had under observation during that summer, eleven were kept in windows facing south and the remaining two in a window which faced north. Like Lie-Pettersen (p. 18), I found that on every warm day, especially if the weather was sultry, one or more workers in each of the colonies on the south side of the building mounted to the top of the nest and began to fan shortly after the rays of the sun reached the nest-boxes. In a colony of *Bremus impatiens*, consisting of about 125 individuals, the number of fanning workers sometimes even increased to more than a dozen. As soon as the sun receded from their nest-box, these "trumpeters" discontinued their work, one after another, and crawled back into the nest.

⁵*Bremus affinis, bimaculatus, fervidus, impatiens, pennsylvanicus, perplexus, separatus, ternarius, terricola, and vagans.*

While this restless activity was in progress on the south side of the building, not a single bee, as a rule, was engaged in "trumpeting" in the two colonies which were kept on the north side, although one of the latter—also belonging to *Bremus impatiens*—consisted of more than 450 workers. The exposure to the hot midday sun evidently did not agree with the bees, for the colonies on the south side of the building did not thrive nearly so well as those on the north side, and during the following summer all of my bumblebee colonies were therefore kept in shady situations.

While "trumpeting" in a bumblebee colony is most pronounced when the nest is exposed to the rays of the sun on a hot day, it may, as is indicated by the observations of Goedart (1685), de Pluche (1764), Hoffer (1882-83), Bengtsson (1903), and Bachmann (1915, 1916), also take place in the morning and evening, in fact, as Wagner (1907) has pointed out, at any time of the day. Thus, for example, I have occasionally found one or two workers fanning at various hours during the night, even if the temperature outside was less than 70°. In this case, as has been suggested by von Buttel-Reepen (1903), fanning no doubt has to do with the expulsion of moisture or disagreeable odors from the nest.

Neither is it true, as Hoffer (1882-83), von Buttel-Reepen (1903), and Sladen (1912) assume, that "trumpeting" is resorted to only by species which have subterranean nests. Wagner (1907) found that *Bremus muscorum*, a European species which usually nests on the surface of the ground, resorts to fanning when the temperature of the nest gets too high, and this, as will be seen later, is also true of *Bremus fervidus* in this country.

As already stated, Hoffer (1882-83) believed that small *Bremus* colonies have no "trumpeter." Wagner (1907) and Lindhard (1912), on the other hand, claim that small colonies also resort to fanning. In order to determine which one of these claims is correct, the following experiment was performed. At 2 P. M., on June 3, 1922, I exposed the next-box of a small colony (1 queen and 2 workers) of *Bremus impatiens* to the rays of the sun. Three minutes later, one of the workers crawled to the top of the nest and began to fan, and within another minute, the remaining worker and the queen appeared and assisted in this activity.

Later in the summer, an experiment was also carried out to test Pérez' (1889) theory, according to which the so-called bumblebee trumpeters are newly emerged individuals which are exercising their wing muscles. On August 14th, at 1.30 P. M., I removed the board which shaded the nest of a queenless colony of *Bremus fervidus* so that the nest-box was exposed to the sun. The result was as follows: At 1.34, a worker appeared on top of the nest, and after crawling about a few seconds, began to fan vigorously. By 1.36 two more workers were engaged in this work, and by 1.38, the number of "trumpeters" had increased to six. All of these "trumpeters", as the hardened pollen lump on the thorax showed⁶, were old bees which had done considerable foraging. *Bremus fervidus* usually nests on the surface of the ground, and hence this experiment incidentally also shows that Hoffer (1882-83), von Buttell-Reepen (1903), and Sladen (1912) are wrong in assuming that only "subterranean" species have "trumpeters."

Summary and Conclusions.

1. The so-called trumpeters in bumblebee colonies are bees which are engaged in ventilating the nest.
2. This ventilation is brought about by a rapid vibration of the wings and may take place at any time during the day or night.
3. Species which nest on the surface of the ground likewise make use of this method of ventilating their nests.
4. Ventilation by fanning is also resorted to by small bumblebee colonies.
5. Pérez' theory, according to which the so-called trumpeters in bumblebee colonies are newly emerged individuals which are exercising their wing muscles, is not founded upon facts.

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⁶The source of these pollen lumps will be discussed in connection with another paper.

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